# SIGNIFICANCE OF DIPLOPOD ACTIVITY IN LEAF LITTER DECOMPOSITION

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## INTRODUCTION

Diplopods are known as an effective group of soil saprophaga which participates in leaf litter decomposition. They feed on leaf litter. During the passage along the digestive tract of diplopods plants remains are macerated and mixed with mineral soil particles.

Diplopods belong to the « primary decomposers » of the forest litter because they can consume the leaves which have not undergone structural destruction (DUNGER, 1958; ZACHARIAE, 1965). But they prefer to feed on the weathered fallen leaves in the lower layer of the forest litter already treated by microorganisms (VAN DER DRIFT 1951; GERE, 1956). The chemical changes in plant tissues effected by diplopods have been found to be very small. This is why the authors investigating the feeding activity of diplopods have assumed that these invertebrates are mostly responsible for the structural decomposition of leaf litter.

The population density of diplopods in broad-leaved forests of some regions of the U. S. S. R. with a temperate and warm climate is comparatively high (up to a few dozen specimens/m²). The diplopod activity in the such forests seems to be the important factor of leaf litter decomposition. The present paper is concerned with a study of diplopods' activity in deciduous forests of the Caucasus. The feeding rate and food assimilability in diplopods as well as the chemical changes in plant tissues in the digestive tract were investigated.

## STUDY AREAS

The study was made in two Caucasus regions. The first was in mixed forests on the Northern slope of the main Caucasus mountain ridge (Maikop region, altitude 600-700 m). The main tree species are beech (*Fagus sylvatica*), silver fir (*Abies alba*)

and hornbeam (*Carpinus betulus*). Oak (*Quercus robur*) and maple (*Acer platanoides*) also occur. The mountain forest brown soils are distributed under the forests (GOLGOFSKAJA *et al.*, 1967).

The second investigation area was in the subtropical deciduous forests of Talysh in the Eastern Transcaucasus (Lenkoran region, altitude up to 300 m). The zheltozem soils are distributed there in the low mountain zone under the forest. The main tree species are oak (*Quercus castanaeifolia*), ironwood (*Parrotia persica*) and hornbeam (*Carpinus betulus*) (GROSSGEIM, 1946).

## MATERIAL AND METHODS

Black wireworms are the predominating group of litter invertebrates in both the regions under investigation. In the forests of the Northern Caucasus 3 species of Julidae were the most numerous : *Pachyiulus foetidissimus* (MUR.), *Cylindroiulus ruber* (LIGNAU) and *Julus colchicus* LOHM.). Diplopods concentrate on the slopes with a humid but not swampy soil. The population density of diplopods in these sites averaged 30-60 spec./m² (STRIGANOVA, 1969).

*Amblyiulus continentalis* ATT. was the predominating species in the forests of Talysh. Its population density averaged 40-60./m².

The comparisons of feeding rate and assimilability of food were carried out under laboratory conditions. 4 litters (overwintered fallen leaves of beech, oak, maple and hornbeam) were used for investigating the feeding rate of Diplopods from the Northern Caucasus. In *A. Continentalis* the consumption rate of oak (*Q. castanaeifolia*) and ironwood was investigated. Food assimilability was evaluated in *P. foetidissimus* (for the oak and hornbeam litters) and *A. continentalis* (for oak and ironwood litters).

The methods of these laboratory investigations were described in the previous papers (STRIGANOVA, 1967, 1969 *a*). The assimilability of food (« A ») was expressed as the p. 100 ratio of assimilated food to consumed food (« C » — consumption). Assimilated food — is the difference between the consumed food and excrements (« FU » — rejecta). For the designation of these indices the symbol system was used proposed at the Conference « Secondary productivity of terrestrial ecosystems » (PETRUSEWICZ 1967).

$$A = \frac{C - FU}{C}$$

Values for the consumed food and excrements were expressed in mg dry weight.

The cellulose content in the different litters and excrements of diplopods was compared. The methods of quantitative investigations of the cellulose content in the plant remain was described earlier (STRIGANOVA, 1970).

## FEEDING ACTIVITY OF DIPLOPODS IN THE NORTHERN CAUCASUS

The diplopods of all 3 species under consideration actively consumed the overwintered leaf fall of beech, oak, maple and hornbeam. Data on the rate of litter destruction are given in Table 1.

The highest rate of food consumption was observed when diplopods were fed on the mixture of different leaf litters. These data allow the assumption that Diplopods under natural conditions in the Maikop region are able to consume up to 400 kg of leaf litter/1 ha/1 month. So they can decompose practically the whole of the leaf fall in the course of their spring and autumn activity. In the early summer the soil was covered with the 0,5-1 cm layer of Diplopod excrements. In the middle of June most of the leaf fall was destroyed except beech litter which diplopods ate at a much slower rate than other kinds of litter.

Diplopods showed a distinct selection with respect to different leaf litters. Beech litter was disliked by the wire worms of all 3 species. Diplopods ate hornbeam litter most actively whereas the rates of consumption of oak and maple litters were intermediate. This tendency was observed when diplopods were fed with a mixture of

TABLE 1

| Litters | Amount of litter dry weight/consumed by 1 specimen/24 h | | | | | |
|---|---|---|---|---|---|---|
| | In uniform litter | | | In mixed litter | | |
| | *P. foetidissimus* | *J. colchicus* | *C. ruber* | *P. foetidissimus* | *J. colchicus* | *C. ruber* |
| Mixture of 4 litters | | | | 52.0 | 12.5 | 12.3 |
| Beech | 12.0 | 1.0 | 1.1 | — | — | 1.1 |
| Oak | 22.0 | 3.3 | 2.5 | 12.0 | 1.0 | 1.5 |
| Maple | 36.0 | 11.0 | 6.1 | 16.0 | 2.0 | 2.5 |
| Hornbeam | 42.0 | 14.0 | 11.3 | 24.0 | 9.5 | 7.3 |

4 litters as well as with uniform leaf litter (table 1). *J. colchicus* and *P. foetidissimus* in the mixed fall did not consume beech litter at all. *C. ruber* ate about 1 mg/24 h. of the beech litter which seemed to be unpalatable because of its chemical peculiarities (STRIGANOVA, 1969 *b*).

The assimilability of the oak and hornbeam litters by *P. foetidissimus* was calculated (STRIGANOVA, 1969 *a*). The results revealed that the average assimilability of hornbeam is 39.4 p. 100 and that of oak-37.6 p. 100 So the diplopods assimilated almost one third of the consumed food.

## FEEDING ACTIVITY OF DIPLOPODS IN TALYSH

The autumn feeding activity in *A. continentalis* was investigated. The rates of decomposition and assimilability of *Q. castanaeifolia* and ironwood litters were evaluated. In October-November diplopods decomposed actively the rest of the

TABLE 2

| | Amount of litter dry weight/consumed by 1 specimen/24 h | |
|---|---|---|
| | Unweathered litter | Old litter |
| Ironwood | 8,9 | 9,0 |
| Oak (*Q. castanaeifolia*) | 5,4 | 18,0 |

last year's fall accumulated in hollows ; at the same time diplopods fed also on the newly fallen leaves which were hardly attacked by micro-organisms. Table 2 shows the feeding rates of the old and unweathered litters.

The feeding rate of the ironwood litter was almost the same irrespective of the degree of its degradation. The rate of consumption of the old litter of *Q. castanaeifolia* was 3 times higher than that of the unweathered one. *A. continentalis* destroyed old oak litter more actively than the ironwood leaf litter. These diplopods can destroy up to 250 kg of leaf litter/ha/month under natural conditions.

The assimilability of old ironwood fall by *A. continentalis* averaged 43 p. 100 of that of oak litter — 31 p. 100 only.

## THE BREAKDOWN OF CELLULOSE BY DIPLOPODS

NIELSEN (1962) found a comparatively high activity of different carbohydrases in diplopods. He found cellulase activity in Polydesmidae representatives only. We found cellulase activity in the hind gut of *P. foetidissimus* (STRIGANOVA, 1971). The presence of this enzyme in black wireworms gives grounds to believe that those invertebrates can digest a part of cellulose in plant remains. The cellulose content in leaf litters from the Northern Caucasus and in the excrements of diplopods was compared. The excrements were collected for these analyses under laboratory conditions. The Diplopods were fed on different litters cleaned previously of mineral particles and detritus. Excrements were taken out twice a day, fixed with toluene to reduce the microbial activity and dried in an oven. The results of analyses are presented in the table 3.

TABLE 3

| | % cellulose content | | | |
|---|---|---|---|---|
| | Control | Excrements | | |
| | | *P. foetidissimus* | *C. ruber* | *J. colchicus* |
| Hornbeam | 18.5 | 11.1 | 5.0 | 12.9 |
| Maple | 19.8 | 5.8 | 11.7 | |
| Oak | 28.3 | 4.3 | 9.1 | |
| Beech | 33.3 | 9.7 | | |

The data show that diplopods digest more than half of the cellulose content of their food. If the cellulose amount in a leaf fall is assumed to be 100 p. 100, *P. foetidissimus* digest 40 p. 100 of cellulose in the hornbeam litter, 70 p. 100 — in the maple, 40 p. 100 — in the oak and 72 p. 100 — in the beech litter. The dayly consumption of cellulose for *P. foetidissimus* is 3-5 mg. Thus the diplopods are the active decomposers of cellulose and thereby they promote the mineralization of organic matter. The ash content in diplopod excrements was found to be higher than that of the leaf litter consumed (SOKOLOV, 1955).

## DISCUSSION

The feeding rate has been used as the main criterion of food preferendum (LYFORD, 1943 ; DUNGER, 1958, 1963 ; WITTICH, 1953 ; SATCHELL, LOWE, 1967). It has been shown to depend on such factors as calcium content, nitrogen content, C/N ratio and content of polyphenolic substances especially tannins.

The mechanical strength of leaf-cuticle thickness and degree of sclerotization of cell walls also influence on the feeding rate. For example diplopods decomposed the oak litter comparatively slower than other litters. But the consumption of oak leaves increased significantly after they had been reduced to fragments by scissors (STRIGANOVA, 1967).

Invertebrates partly digest plant tissues causing significant chemical changes in organic remains. The assimilability of food characterizes the degree of its fitness, i. e. the nutritiousness. Theoretically the assimilability of food should be inversely proportional to the rate of food consumption. In practice the rate of food consumption depends on some other factors mentioned above. For example, the assimilability of oak and hornbeam litters by *P. foetidissimus* is almost the same, but the rate of hornbeam litter consumption is 1,5 times as high as that of oak.

Thus, in the studies of food preferendum of soil invertebrates it is necessary to investigate not only the feeding rate but the assimilability of food also. The feeding rate characterizes the mechanical destruction of leaf litter, whereas the assimilability of food shows the degree of its chemical decomposition.

## CONCLUSIONS

Diplopods play a great role in leaf litter decomposition in the regions where they are abundant. In the Caucasus their population density reaches a few tens/m² and they appear to be the predominating group of invertebrates among forest-litter dwellers. Diplopods are able to decompose there hundreds of kilograms of leaf fall during one season. They macerate plant remains and create a great surface available for microfauna and microorganisms. Diplopods actively digest carbohydrates and proteins assimilating 30-40 p. 100 of the food consumed. Diplopods decompose cellulose especially actively (more than half of the cellulose content in leaf tissues) and thereby they promote the mineralization of the plant remains.

Thus diplopod activity in forest litter seems to be an important factor accelerating turnover in forest biocenoses and increasing their productivity.

## ZUSAMMENFASSUNG

BEDEUTUNG DER TAUSENDFÜSSLERAKTIVITÄT IN DER LAUBSTREUZERSETZUNG

In den Misch- und Laubwäldern des Kaukasus sind die Tausendfüssler (Julidae) sehr zahlreich. Ihre Populationsdichte erreicht dort 60 Ind./m². Es wurden Untersuchungen über die Aktivität der Laubstreuzersetzung und Nahrungsausnützung durchgeführt. Im Laufe des Jahres können die Tausendfüssler Hunderte kg der Laubstreu verarbeitern. Sie zerkleinern und mazer-

ieren die Blattgewebe und assimilieren etwa 30-40 p. 100 der aufgenommenen Nahrung. Im Darmtrakt der Tausendfüssler wurde Abbau der Zellulose festgestellt. Sie können den grössten Teil der Zellulose in Blattgeweben zerlegen (40-80 p. 100). Diplopoden sind nicht nur für die mechanische Zersetzung der Laubstreu verantwortlich, sie beteiligen sich auch unmittelbar in der Mineralisierung der Laubstreu.

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## DISCUSSION (1)

G. MARCUZZI : Asks whether cellulose is produced by animals or by intestinal microorganisms.

Observes that probably the species investigated by Striganova can consume all cellulose present since *Glomeris* also behaves so.

M. S. GHILAROV : Probably by microorganisms.

J. VAN DER DRIFT : 1° The assimilability of hornbeam leaves of *P. foetidissimus* seems rather high. Is this a common occurrence with your millipedes ?

(1) En raison de l'absence de l'auteur, cette communication a été présentée par G. ZACHARIAE.

1° Is there selectivity in feeding of this millipede between the different parts of the leaf by which the comparability of cellulose content of food material and excrement can be influenced?

B. STRIGANOVA : 1° The assimilability of hornbeam litter by millipedes ranged between 30 and 40 p. 100 in experiments with *P. foetidissimus*, *A. continentalis* and *S. kessleri*. Adult specimens of *P. flavipes* have the lower assimilability-19-26 p. 100.

The assimilability does not depend on the amount of food supplied.

2° The millipedes do not consume thick ribs and parenchyma tissues near the bases of the leaves. In laboratory experiments the tops of leaves only were used both for feeding of animals and for control measurements of cellulose content.

P. BERTHET : In connection with Dr van der Drift's remark, I should like to point out that Dr O. Paris (*Proceedings of the Secondary Productivity*, Warsaw) observed in Isopods, that the percentage of the assimilated food may vary considerably according to the quantity of available food and thus according to the speed of the passage of the food through the digestive tract.

M. S. GHILAROV : Really the amount of food consumed by saprophagous Arthropods depends on the tree species, of which the foliage becomes litter and on the way and degree of the microbial decomposition of these leaves.

On these both properties of food depends its palatability. As a rule the more abundant and various is the food, the higher is its consumption.

C. A. EDWARDS : I should like to ask about the term « overwintered leaves of beech, oak, maple and hornbeam ». It is well known that leaves become more palatable to invertebrates with aging and it is important to know now how old the leaves fed to millipedes were.

I should also like to know if the figures in table 1 represent percentage of dry weight consumed per 24 hours.

G. ZACHARIAE : The leaves fell in autumn, and certainly Dr Striganova collected them half a year later in spring. So these leaves have been leached by winter precipitation, and some microbial fermentation may have occurred in the first warm weeks after winter.

The figures in table 1 give the absolute amount of dry weight of litter consumed per individual and day.

D. M. WEBLEY : Was lignin of leaf material digested?

M. S. GHILAROV : Lignin is not digested.

U. BABEL : Zur Ligninzersetzung von Bodentieren, besonders Diplopoden : Bodendünnschriffe zeigen in Exkrementen unveränderte Blaufluoreszenz von Lignin.

B. STRIGANOVA : Die Tausendfüssler wie auch andere Bodensaprophaga zersetzen nicht das Lignin, doch im tierischen Darmkanal findet die Herauslösung des Lignins aus dem Zellulosemverband statt.

T. G. WOOD : The comment of Dr Zachariae is probably true although the work of Siefert and Becker indicates that termites are capable of digesting lignin. As far as Dr Striganova's results are concerned, if millipedes are capable of digesting more than 50 p. 100 of the cellulose in leaf litter the activity of these animals may have profound effects on soil micro-organisms. The majority of soil animals cannot digest cellulose or can do so to only a limited extent. Termites are a notable exception being able to digest up to 80 p. 100 of the cellulose in plant tissue. Investigations on the wood-feeding *Nasutitermes exitiosus* in Australia by Dr K. E. Lee and myself have shown that the faecal material, which is the dominant constituent of certain regions of the nests of this species, is very resistant to decomposition. Chemically the faeces are relatively low in cellulose and high in lignin and Dr J. Stout has shown that microbial respiration in abandoned termitaria of this species is very low and it appears that the faecal material is toxic to micro-organisms. The comminution of leaf litter by millipedes is generally believed to stimulate microbial activity, but if they do digest a large proportion of the cellulose, leaving the more resistant materials such as lignin, their faeces may be an unfavourable substrate for many micro-organisms.

B. STRIGANOVA : Excrements of many invertebrates including diplopods are indeed the centres of microbial activity in soil. But the composition of microflora in excrements considerably differs in several groups of invertebrates in connection with the peculiarities of their digestion. Investigations of L. S. KOZLOVSKAJA (1962, 1968, 1970) showed that the intensive development of bacteria which utilize nitrogen from organic and mineral compounds was observed in excrements of diplopods; cellulose-destroying microorganisms are stimulated by diplopods very slightly.